Changes in understory composition following catastrophic windthrow and salvage logging in a subalpine forest ecosystem

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Abstract: Catastrophic windthrow and postdisturbance salvage logging each have the potential to profoundly influence understory vegetation communities. This study compared understory vegetation cover, composition, and diversity in Routt National Forest, a subalpine forest in northwestern Colorado that sustained a 10 000 ha blowdown in 1997 and was partially salvage logged in 1999. Understory and edaphic variables were measured in five heavily wind-disturbed *Picea–Abies* stands, five stands salvage logged 20 months after the blowdown, and five intact stands. Understory species cover and diversity were greater in blown down areas than in salvage-logged or control areas. Community composition of each treatment area was distinct and related to a gradient in organic soil depth, which reflected the severity of understory disturbance. Composition and diversity in blowdown areas relative to control areas stabilized in the 5 years following the blowdown, but vegetation cover continued to increase. Blowdown areas contained early and late successional species. Salvage-logged areas exhibited a shift towards graminoid dominance. This structural change could delay future conifer seedling establishment. The interaction among disturbance severity, understory vegetation composition, and regeneration dynamics should be considered in future decisions to salvage log similar areas because the long-term effects of salvage logging are unknown.

Résumé : Le chablis catastrophique et la coupe de récupération après une perturbation ont chacun la possibilité de sérieusement influencer les communautés végétales de sous-bois. Cette étude a comparé le recouvrement, la composition et la diversité de la végétation de sous-bois dans la forêt nationale de Routt, une forêt subalpine du nord-ouest du Colorado qui a subi un chablis de 10 000 ha en 1997 et une coupe de récupération partielle en 1999. Des variables édaphiques et de sous-bois ont été mesurées dans cinq peuplements de *Picea* et d'*Abies* sévèrement perturbés par le vent, cinq peuplements ayant subi une coupe de récupération 20 mois après le chablis et cinq peuplements non perturbés. La diversité et le recouvrement des espèces de sous-bois étaient plus élevés dans les zones affectées par le chablis que dans les zones témoins ou ayant subi une coupe de récupération. La composition de la communauté végétale de chaque zone de traitement était différente et reliée à un gradient dans la profondeur du sol organique qui reflétait la sévérité de la perturbation du sous-bois. La composition et la diversité dans les zones affectées par le chablis relativement à celles des zones témoins s'étaient stabilisées 5 ans après le chablis mais le recouvrement de la végétation a continué à augmenter. Les zones affectées par le chablis contenaient des espèces de début et de fin de succession. Les zones qui avaient subi une coupe de récupération évoluaient vers une dominance des graminées. Ce changement structural pourrait retarder l'établissement futur de semis de conifères. L'interaction entre la sévérité de la perturbation, la composition de la végétation de sous-bois et la dynamique de la régénération devrait être considérée lors de décisions futures de procéder à une coupe de récupération dans des endroits similaires parce que les effets à long terme de la coupe de récupération ne sont pas connus.

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Introduction

Catastrophic windthrow is a dominant, although infrequent, form of disturbance in many temperate forest ecosystems (Canham and Loucks 1984; Foster and Boose 1992; Peterson and Pickett 1995; Everham and Brokaw 1996; Webb 1999). Such canopy disruption often increases light availability (Bellingham et al. 1996), increases heterogeneity in soil nutrients (Carlton and Bazzaz 1998), and alters edaphic characteristics as a result of pit and mound microtopography created by uprooted trees (Beatty and Stone 1986). Increased light levels and environmental heterogeneity create an opportunity for colonizing species to enter the disturbed community and frequently results in greater understory species diversity (Peterson and Pickett 1995), a shift in the distribution of species among growth forms

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(Zamora 1982), and acceleration of succession by release of shade-tolerant subcanopy trees from overstory suppression (Veblen et al. 1989; Webb and Scanga 2001).

In heavily blown-down forests, removal of commercially valuable timber is often used to generate revenues from damaged trees, reduce fuel loads, or facilitate reforestation efforts (Gorte 1996; McIver and Starr 2000). The United States Healthy Forest Restoration Act (US Congress 2003) authorizes expedited fuel reduction practices, including salvage logging, on federal lands that have experienced windthrow, ice storm damage, fire, and other large-scale disturbances. Such practices are also common outside of North America (Fischer et al. 1990; Van Nieuwstadt et al. 2001; Lindenmayer et al. 2004), where the practice is sometimes called "sanitary logging." Although both economic and ecological reasons are used to justify removal of valuable timber from wind-disturbed forests, few studies have examined the effects of this management practice. Moreover, the studies that have examined this practice suggest salvage logging can result in significant changes to vegetation communities.

For example, northeastern US forests experienced an acceleration of succession following a large hurricane in 1938, which created canopy openings that released shade-tolerant understory from overstory suppression (Spurr 1956). Subsequent salvage logging, which was widespread, resulted in an influx of pioneer species that delayed succession (Spurr 1956). Similarly, in a blown down *Pseudotsuga–Tsuga–Abies* forest in Oregon, salvage logging favored the establishment of shade-intolerant species, whereas regeneration of unlogged areas resulted in dominance of shade-tolerant species (Sinton et al. 2000). Salvage logging of a blown-over Norway spruce (*Picea abies* (L.) Karst.) forest in Bavarian Forest National Park, Germany, resulted in a proliferation of pioneer species and regeneration dominated by birch (*Betula* spp.), while 5 years after the storm, the understory of unlogged areas resembled that of undisturbed areas and was undergoing spruce regeneration (Fischer et al. 1990). In contrast, salvage logging following hurricane disturbance in a southeastern Appalachian forest in the United States resulted in a diverse vegetation community with both early and late successional species relative to communities in undisturbed forested areas (Elliott et al. 2002). However, Elliot et al. (2002) did not examine unlogged hurricane-damaged areas, limiting direct comparison with the other studies.

On 25 October 1997, an unusual blizzard with wind speeds exceeding 200 km/h blew down 10 000 ha of mature subalpine forest in northwestern Colorado (Wesley et al. 1998). The blowdown was the largest recorded in the southern Rocky Mountain region (Wesley et al. 1998). The windstorm created more than 400 patches of downed trees, which ranged from <1 to ~310 ha (Lindemann and Baker 2001). Because such large-scale wind disturbances can cause spruce beetle (*Dendroctonus rufipennis* (Kirby); Coleoptera: Scolytidae) epidemics (Schmid and Frye 1974; Veblen et al. 1991, but see Kulakowski and Veblen 2003), the USDA Forest Service conducted tractor-, cable-, and helicopter-based salvage-logging operations on 935 ha of blown-down forest from 1998 to 2001.

This study compared the effects of the 1997 windstorm and the effects of subsequent salvage-logging activities on understory composition, cover, and diversity. Intact forest areas were evaluated as a control. Indirect gradient analysis was used to identify factors that structure the vegetation communities. Understory community characteristics in disturbed areas provided insight on potential understory trajectories.

Materials and methods

Study area

The study area was Routt National Forest, located in northwestern Colorado (40°47′N, 106°15′W). The dominant canopy species are subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), lodgepole pine (*Pinus contorta* Dougl. ex Loud. var *latifolia* Engelm.), and trembling aspen (*Populus tremuloides* Michx.). Soils are derived from Precambrian granites, gneiss, and glacial deposits (Snyder et al. 1987) and are classified as typic Cryochrepts and Dystrocryepts (USDA Forest Service 1999). A distinct, thin (<6 cm) organic horizon overlies a sandy loam textured mineral horizon. Elevation ranges from 2500 to 2900 m a.s.l. The climate is continental with a mean annual temperature of 3.8 °C, which ranges from a daily mean of –9.6 °C in January to 16.6 °C in July (Colorado Climate Center 2003). Mean annual precipitation is 94 cm, ranging from 63 cm at low elevations to 150 cm at high elevations (USDA Forest Service 1999). Most of the precipitation in this area comes from winter snow and summer monsoons.

Experimental design

The blowdown occurred in October 1997. In May 2000, 15 plots (400 m^2 each) were established. Five plots were in separate unlogged patches of blowdown, five plots were in blowdown patches that were salvage logged with tractors the summer of 1999, and five control plots were in intact forest. All plots were at least 250 m apart on flat areas with <5° slopes to minimize effects of slope, aspect, and topographic position. Blowdown and salvage-logged plots were located in separate patches to minimize pseudoreplication. Blowdown and salvage-logged plots were located in large patches of heavy blowdown damage. Canopy cover in these areas was <10% in May 2000. Control plots were located in areas with >70% canopy cover.

To minimize effects of any predisturbance vegetation differences, plots were located in stands of similar overstory composition and structure. Plots were located in stands dominated by Engelmann spruce and subalpine fir with subdominant lodgepole pine. Adult aspen were never present in a stand. Age structure was approximated by coring large-diameter (>50 cm) intact or fallen canopy trees in control and blowdown areas and by counting tree rings on stumps in salvage-logged areas. Age of these trees ranged between 200 and 250 years, although some were greater than 300 years. Age of large-diameter trees did not differ significantly among treatments. Mean basal area and stem density of control stands ranged from 34 to 58 m^2/ha and from 850 to 1675 stems/ha. Predisturbance basal area data was not available for blowdown or salvage-logged stands. However, these stands were carefully selected to represent a similar range of structural characteristics, as determined wherever possible from intact forest surrounding disturbance patches.

Control and blowdown plots were located at a lower elevation than salvage-logged plots because suitable areas protected from salvage logging were located at lower elevations within the Elk River Scenic Management Area, Routt National Forest, Colorado. Mean elevation of control and blowdown plots was 2560 ± 20 and 2560 ± 8 m a.s.l, respectively, whereas salvage-logged plots were located at 2865 ± 17 m a.s.l. To insure that treatment differences were not confounded with elevation differences, understory composition of intact areas surrounding salvage-logged areas and small patches of protected vegetation within salvage-logged areas were examined where possible. For further aid in comparison, the understory composition of intact spruce–fir forest located 2550–2800 m a.s.l. in a remote section of Routt National Forest was also evaluated. The composition, diversity, and cover of understory vegetation around and within protected patches in salvage-logged areas and in intact higher elevation spruce–fir forests were similar to lower elevation intact stands used as controls in this study. The understory of these areas was dominated by grouseberry (*Vaccinium* spp.), arnica (*Arnica cordifolia* Hook.), silvery lupine (*Lupinus argenteus* Pursh.), elk sedge (*Carex geyeri* Boott.), geranium (*Geranium richardsonii* Fisch & Trautr.), and blue wild rye (*Elymus glaucus* Buckl.), which are species typically associated with mesic spruce–fir forest in Colorado (Peet 1981; Weber and Wittmann 1996). Peet (1981) describes mesic spruce–fir forest in Colorado as "remarkably homogeneous," dominated by *Vaccinum* spp. in the understory, and extending from 2500 to above 3100 m a.s.l. Thus, all plots included in this study are within the elevation range of mesic spruce–fir forest in the Colorado Rockies and likely had similar understory composition prior to the blowdown and salvage-logging disturbances.

To establish that edaphic characteristics did not vary significantly with elevation, plots were only located in flat areas at the foot of slopes to control for topographic position and slope, which may influence soil properties as organic horizon depth. Soil organic horizon depth was measured in intact spruce–fir forest across an elevation gradient in Routt National Forest and combined with organic horizon depth and elevation data reported in studies of other Colorado spruce–fir forests. The resulting graph (Appendix A, Fig. A1) shows no relationship between organic horizon depth and elevation, which suggests that, at a large spatial scale, factors other than elevation control organic horizon depth in these forests.

Collectively, these observations suggest that understory vegetation and edaphic differences between salvage-logged and other treatments may be assumed, with appropriate caution, to result from salvage logging rather than exclusively a consequence of elevation differences. However, elevation may amplify the treatment differences detected in this study.

Vegetation sampling occurred in 2001 and 2002, when blowdown plots were in their fourth and fifth year of recovery after the original disturbance, and salvage-logged plots were in their second and third year of recovery following logging. The study could not be extended to compare vegetation recovery after a standard period of time (i.e., 4 or 5 years) in both disturbed treatments as initially planned because a large wildfire consumed the study area in August 2002. The effects of the blowdown and salvage-logging disturbances on postfire regeneration patterns is the subject of another study (C.M. Rumbaitis del Rio and C.A. Wessman, unpublished manuscript).

Field measurements

Eight 0.25 m^2 vegetation quadrats were randomly located within each 400 m^2 plot in July 2001 and 2002. Understory vegetation cover was estimated visually within each quadrat for each species encountered, according to the Braun–Blanquet method (Kent and Coker 1996). Cover values were averaged to the nearest 5%. The quadrat was divided into 10 cm × 10 cm grid sections to facilitate visual estimates. Understory species included all forbs, graminoids, shrubs, and nonvascular plants, but not subcanopy tree species. Percent cover also was determined for bare mineral soil, litter (decomposing leaf material and fine woody debris), and coarse woody debris (diameter > 7.6 cm). *Galium septentrionale* Roemer & Schultes and *Galium trifidum* L. were difficult to differentiate and, thus, were grouped together, as were *Osmorhiza depauperata* Phil. and *Osmorhiza chilensis* Hook & Arn. A few Asteraceae, Liliaceae, Ranunculaceae, and Cyperaceae were not identified to species because of missing flowering parts. All mosses were grouped into a single Bryophyta category. Nomenclature follows Weber and Wittmann (1996). Species were classified into life forms with the USDA PLANTS database (USDA Natural Resources Conservation Service 2004).

Soil samples 10 cm deep and 300 cm^3 in volume were collected from 10 random locations in each 400 m^2 plot. The samples contained both the organic horizon and mineral soil, if an organic horizon were present. Depth of the organic soil horizon was measured in the field and horizons were kept separate. Soil pH was determined in a 2:1 distilled water – dry soil slurry (Robertson et al. 1999). Soil texture was measured using the hydrometer method (Elliott et al. 1999). Total soil nitrogen content of the organic and mineral component of each sample were measured on sieved, dried, and hand-ground subsamples using an Eager 1108 CHN elemental analyzer (Sollins et al. 1999). Total nitrogen in the top 10 cm of soil was estimated by weighting the nitrogen content of each horizon by its depth.

Statistical analysis

Percent cover data from eight 0.25 m^2 quadrats located in each plot were averaged and used to calculate plot-level species richness, evenness (Pielou's *J*), Shannon–Wiener diversity, cover and proportional cover of forbs, graminoids, shrubs, and nonnative species for 2001 and 2002. Gamma (γ), or landscape-level diversity, was the total number of species in each treatment.

A mixed-model repeated measures analysis of variance (ANOVA) was used to detect differences in treatment, time, and treatment × time interactions among diversity indices, % cover, nonnative species cover, and proportional vegetation cover in each growth form (SAS Institue Inc. 2001). Treatment was specified as a fixed factor; plot and year were random factors. Treatment differences in understory and edaphic characteristics were assessed using ANOVA. Tukey Studentized range multiple comparison tests were used to interpret individual treatment differences where they occurred. Shrub cover and proportional shrub cover were arcsine

Table 1. Understory and edaphic variables in the three treatment areas.

Parameter	Treatment: Blowdown	Control	Salvage logged	ANOVA p values
Organic horizon depth (cm)	6.12±0.86a	4.15±0.44a	1.48±0.42b	0.0003
Nitrogen content (g N/m^2)				
Organic horizon	242±39.8a	145±35.1ab	43±18.6b	0.0035
Mineral soil	76±32.7a	142±21.9ab	234±36.3b	0.0230
Top 10 cm	317±29.9	287±20.7	277±30.6	ns
Soil pH	5.8±0.17	5.5±0.10	5.3±0.09	ns
Sand fraction (%)	63.7±4.6	61.3±2.7	54.8±2.5	ns
Silt fraction (%)	31.9±4.6	33.4±2.4	39.1±1.5	ns
Clay fraction (%)	4.5±0.7	5.3±0.3	6.2±1.1	ns
Bare area cover (%)	2±0.6a	14±6.6a	25±16.7b	0.0002
Litter area cover (%)	8±1.6a	37±9.1b	12±4.9a	0.0053
Coarse wood area cover (%)	27±4.2a	5±2.2b	33±6.0a	0.0003

Note: Values are means ± SE (N = 5 plots per treatment). ANOVA p values are for comparisons among treatments. For significant ANOVAs, values with different letters among treatments are significantly different (Tukey's Studentized range test, α = 0.05). ns, not significant.

square-root transformed prior to analysis to achieve normality of residuals and homogeneity of variances.

Differences in species composition among treatments and between years were evaluated using the multiresponse permutation procedure (MRPP), a nonparametric multivariate procedure that tests the null hypothesis of no difference between two or more groups (McCune and Grace 2002*a*). Quadrat data from within plots were pooled. Percent cover data were arcsine square-root transformed, and species with only one occurrence were excluded from the MRPP analysis but were included in calculating diversity indices. The mean distance within and among groups was calculated using the Sørensen distance measure. When treatment was significant, specific differences were identified by repeating the MRPP analysis comparing two treatments at a time, using Bonferroni corrections. Indicator species analysis was used to describe species relationships to the three treatments (McCune and Grace 2002*b*). The indicator value of each species was tested for statistical significance using a Monte Carlo randomization technique with 1000 permutations.

A nonmetric multidimensional scaling procedure (NMS) was used to ordinate plot data (McCune and Grace 2002*c*). NMS is an iterative searching procedure that reduces the dimensionality of the dataset by reducing "stress", an inverse measure of goodness-of-fit (McCune and Grace 2002*c*). Input data was the same as for MRPP. The dimensionality of the data set was selected as the point at which additional dimensions no longer reduced final stress by more than five units (on a scale from 0 to 100) and where the final stress of 50 runs of the data was lower than the final stress of at least 95 of 100 runs of randomized data in a Monte Carlo significance test. NMS was then rerun using the solution with the lowest final stress from the prior 50 runs of real data as a starting point. The stability of the final solution was determined by calculating the standard deviation of stress in the last 10 iterations, which was less than 10^{-4}, signifying a reliable ordination (McCune and Grace 2002*c*). The variance represented was expressed as the coefficient of determination among distances in the reduced NMS space and distances in the original species space, using the Sørensen distance measure. Pearson product–moment correlations between environmental variables and ordination scores were depicted in joint plots, where vectors were superimposed on the ordination indicating the direction and strength of the relationship. PC-ORD (McCune and Mefford 1999) was used to conduct MRPP, indicator species, and NMS analyses.

Results

Understory and edaphic variables

There were few differences in the understory environment of control and blowdown treatments, but larger differences occurred between blowdown and salvage-logged treatments (Table 1). The depth of the organic soil horizon was shallower and the coverage of bare mineral soil was greater in salvage-logged areas than in control or blowdown areas. Differences in organic horizon thickness led to differences in the total nitrogen content of the organic horizon and mineral fraction, but not in the total nitrogen content of the top 10 cm of soil, as calculated by weighting each sample by the depth of the organic horizon. Greater litter cover was found in control areas than blowdown or salvage-logged areas, whereas salvage-logged and blowdown areas contained a greater cover of coarse woody debris than intact areas. Soil pH and texture did not differ by treatment.

Vegetation diversity, evenness, and % cover

Blowdown areas had greater total understory vegetation cover than control areas but did not have significantly greater Shannon–Weiner diversity (Table 2). Salvage-logged areas had reduced vegetation cover, species richness, and Shannon–Weiner diversity compared with both control and blowdown areas. Total vegetation cover averaged across treatments was greater in 2002 than in 2001, primarily as a result of a 20% increase in total understory vegetation cover in blowdown areas. Total understory vegetation cover in control and salvage-logged areas remained nearly constant between 2001 and 2002.

Forb cover was greater in blowdown plots than in salvage-logged plots (p = 0.0026; Fig. 1*a*), but differences between

Table 2. Understory vegetation diversity and cover.

	Treatment			ANOVA p values		
Parameter	Blowdown	Control	Salvage logged	Treatment	Year	Treatment × year
Species richness	17.8±1.6a	14.6±1.5a	6.3±0.7b	<0.0001	ns	ns
Shannon–Wiener diversity	2.2±0.1a	2.0±0.2a	1.3±0.1b	0.0038	ns	ns
γ diversity*	45	35	15	—	—	—
Evenness	0.76±0.02	0.75±0.04	0.74±0.02	ns	ns	ns
Total vegetation cover (%)	70±6.1a	46±3.6b	22±4.3c	0.0005	0.0105	0.0059
Nonnative species cover (%)	0.8±0.25a	0.1±0.07b	0.4±0.19ab	0.0412	ns	ns
Vaccinium spp. cover (%)	8.7±1.7ab	16±4.4a	6.0±1.4b	0.0411	ns	ns

Note: Values are means ± SEs (N = 5 plots per treatment). ANOVA p values are for comparisons among treatments. For significant ANOVAs, values with different letters among treatments are significantly different (Tukey's Studentized range test, α = 0.05). ns, not significant.

*γ diversity was defined as the total number of species found in each treatment category and is not replicated; thus, it does not have standard error or ANOVA results.

blowdown and control plots were marginal (p = 0.0803) and not significant between control and salvage-logged areas. Forb cover did not change between 2001 and 2002. The proportion of forb cover relative to total vegetation cover did not significantly differ by treatment, year, or their interaction (Fig. 1*b*). Graminoid cover and proportional graminoid cover were greater in 2002 than in 2001 (graminoid cover, p = 0.0077; proportional graminoid cover, p = 0.0022), but did not differ by treatment. The treatment × year interaction in proportional graminoid cover was significant (p = 0.0136). The 112% increase in proportional graminoid cover in salvage-logged areas between 2001 and 2002 was marginally significant (p = 0.0650). Proportional graminoid cover only increased by 45% and 8% in blowdown and control areas, respectively, between 2001 and 2002, which were not significant increases. Shrub cover and proportional shrub cover did not differ by treatment, year, or their interaction, but cover of the dominant understory shrub, *Vaccinium* spp., was lower in salvage-logged areas than in control areas (Table 2). *Vaccinium* spp. cover in salvage-logged areas decreased by 35% between 2001 and 2002.

Community composition

Fifty-four understory species were identified. Of these, 38 were forbs, 9 were shrubs, and 7 were graminoids (Table 3). Almost all species encountered were perennials, except for a few weedy species such as *Vicia villosa* Roth. and *Spergularia rubra* (L.) J & K Presl., which have variable growth cycles, and *Bromus japonicus* Thunb. and *Collomia linearis* Nutt., which are annuals.

Five nonnative species were found. Nonnative species cover was low in all treatments, but was significantly greater in blowdown areas than in control areas (Table 2). Proportional nonnative cover was marginally greater in salvage-logged areas than in control areas (p = 0.0678), but did not differ between salvage-logged and blowdown sites.

MRPP tests showed that understory composition was distinct for all treatments (p < 0.0005 for all treatment comparisons) and did not differ among years. *Calamagrostis canadensis* (Michx.) Beauv., *Distegia involucrata* (Banks ex Sprengel) Cockerell, *Elymus glaucus*, *Galium* spp., *Geranium richardsonii*, *Ligusticum porteri* Coulter & Rose, *Oreochrysum parryi* (Gray) Rydb., *Rosa woodsii* Lindl., and *Thalictrum fendleri* Engelm. ex Gray were significant indicator species for blowdown areas, although some of these were also found in control and salvage-logged areas. Most of these species are typically found in subalpine forests, aspen groves, and moist meadows (Weber and Wittmann 1996). Indicator species for control areas were *Arnica cordifolia*, *Pseudocymopterus montanus* (Gray) Coult. & Rose, *Lathyrus leucanthus* Rydb., and Bryophyta, which are typically found in dry subalpine forests (Weber and Wittmann 1996). The only indicator for salvage-logged conditions was *Carex rossi* Boott in Hook., which is widely distributed from the foothills to dry subalpine areas in Colorado (Weber and Wittmann 1996).

The NMS ordination of plot data showed distinct clusters of plots by treatment (Fig. 2*a*). Clustering is greater for salvage-logged plots than for blowdown and control plots, which overlap partially. This suggests there was greater homogeneity in species composition among salvage-logged areas than in either control or blowdown areas. The final solution for the NMS ordination was two-dimensional and significant (p = 0.0196). The coefficient of determination between ordination distances and distances in the original dimensional space was 0.24 for NMS axis 1 and 0.58 for NMS axis 2. The two axes explained 82% of the variance.

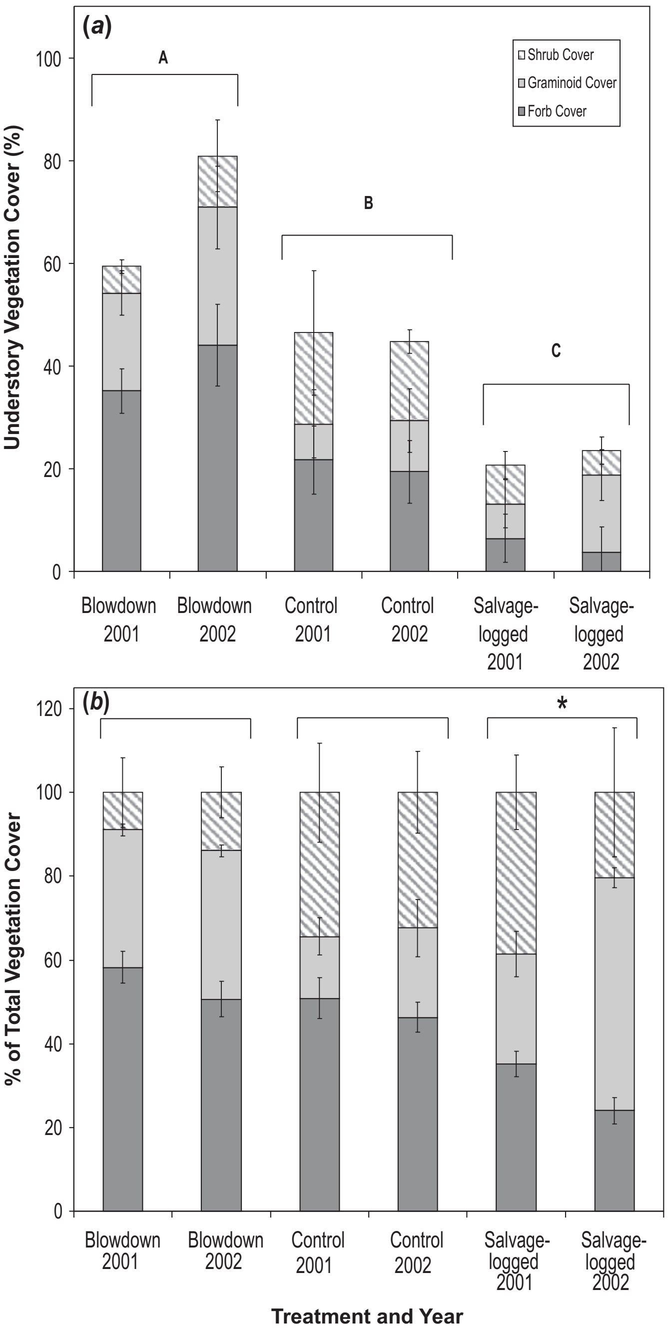
Depth of the organic horizon, total nitrogen content of the organic horizon, and % forb cover were positively correlated with NMS axis 2 (r^2 > 0.64; Fig. 2*a*). These three variables were also positively correlated with each other (r^2 > 0.64). Elevation was negatively correlated with both axis 1 and axis 2 (r^2 > 0.36 for both axes). No other variables were significantly correlated with either NMS axis. There was no trend in compositional change for control plots between 2001 and 2002; however, most blowdown and salvage-logged plots showed a decrease in axis 1 scores and an increase in axis 2 scores between 2001 and 2002 (Fig. 2*b*).

Discussion

Species diversity and cover and disturbance severity

At the plot level, understory diversity did not differ between intact and blowdown areas, but γ, or landscape-level, diversity was nearly 30% greater in blowdown areas than in control areas. The increase in diversity found in this study was modest compared with studies of other blowdown forest ecosystems, where species richness is initially enhanced by

Fig. 1. (*a*) Percent understory vegetation cover by growth form, treatment, and year and (*b*) percentage of total vegetation cover in each growth form category by treatment and year. Means are ± 1 SE (N = 5 for each treatment and year combination). Uppercase letters in Fig. 1*a* show significant differences among treatments in total % cover averaging across years (Tukey's Studentized range test, α = 0.05). Asterisk in Fig. 1*b* shows significant differences between 2001 and 2002 in distribution of vegetation cover among growth forms within a treatment.



large-scale wind disturbance (Cooper-Ellis et al. 1999; Palmer et al. 2000; Peterson and Pickett 1990, 1995). The smaller difference in diversity between blowdown and intact areas observed in this study may be due to the lower understory diversity and shorter growing season of subalpine forests relative to lower elevation, eastern US mixed conifer–deciduous forests. Similar to other studies of blowdown disturbances (Cooper-Ellis et al. 1999; Palmer et al. 2000; Peterson and Pickett 1995; Reid 1989), this study found greater vegetation cover in blowdown areas than in intact areas and did not detect a shift in the relative abundance of forbs, shrubs, and graminoids. Blowdown areas experienced an increase in cover of early successional species that thrive in disturbed areas, such as *Rubus idaeus* L., *Chamerion danielsii* D. Löve, and *Distegia involucrata*, as well as late successional species such as *Geranium richardsonii*, *Oreochrysum parryi*, and *Thalictrum fendleri*. Although microsite differences were not a focus of this study, field observations suggest early successional species such as *Chamerion danielsii* commonly colonize tip-over mound created by fallen trees, but few species colonize mineral soil dominated root pits, except for the invasive thistle, *Breea arvensis* (L.) Lessing, which appeared to thrive in pit microsites. Similar partitioning of pit and mound microtopography by understory herbs and tree seedlings has been found elsewhere (Beatty and Stone 1986; Kulakowski and Veblen 2003; Peterson and Campbell 1993).

In contrast to both control and blowdown areas, species richness, diversity, and vegetation cover were reduced in salvage-logged areas. Species growing in salvage-logged areas were primarily early successional disturbance specialists such as *Chlorocrepis tristis* (willdenow ex Sprengel) Love & Love subsp. gracilis (Hook.) weber, *Spergularia rubra*, *Chamerion danielsii*, and shade-intolerant species such as *Arnica cordifolia*, *Lupinus argenteus*, and *Carex rossi*. Few shade-tolerant forbs were found in salvage-logged areas, in contrast to the results of Elliott et al. (2002), where a mixture of shade-tolerant and shade-intolerant forbs were found in a salvage-logged mixed-hardwood forest. Gamma diversity in salvage-logged areas was 40% less than in control areas and 66% less than in blowdown areas. At a landscape level, the blowdown added 15 species to the assemblage found in intact spruce–fir forest, whereas salvage logging only added two species not found in the other treatments, one of which (*Spergularia rubra*) is nonnative. From a landscape perspective, the blowdown disturbance helps maintain understory diversity, whereas salvage logging does not initially contribute to understory diversity.

The difference in species diversity and vegetation cover between blowdown and salvage-logged areas in this study could result from sampling salvage-logged areas sooner after disturbance than blowdown areas. Understory composition often fluctuates in the first 3 years following a disturbance (Rydgren at al. 2004; Turner et al. 1997). However, an additional 1 or 2 year recovery period is unlikely to eliminate the differences between salvage-logged and blowdown areas detected in this study because most species found were perennials, which suggests a relatively stable vegetation composition in the short term. Notably, species diversity and total vegetation cover did not increase in salvage-logged areas between 2001 and 2002, as may have been expected if these factors were only a function of time since disturbance. Furthermore, results from longer term studies of logged spruce–fir forests suggest that differences in understory composition and diversity between logged and intact areas

Table 3. List of species found in this study according to treatment and growth form.

Family	Species	Treatment	Growth form
Alsinaceae	*Stellaria calycantha* (Ledeb.) Bong.	B	F
Apiaceae	*Ligusticum porteri*	B, C	F
Apiaceae	*Osmorhiza depauperata* and *Osmorhiza chilensis*	B, C	F
Apiaceae	*Pseudocymopterus montanus*	B, C	F
Asteraceae	*Achillea lanulosa* Nutt.	B, C	F
Asteraceae	*Arnica chamissonis* Lessing subsp. Foliosa (Nutt.) Maguire	B	F
Asteraceae	*Arnica cordifolia*	B, C, L	F
Asteraceae	*Arnica parryi* Gray	B, C	F
Asteraceae	Unknown	B	F
Asteraceae	*Breea arvensis**	B, C, L	F
Asteraceae	*Chlorocrepis tristis*	L	F
Asteraceae	*Erigeron peregrinus* (Banks ex Pursh) Greene	B, L	F
Asteraceae	*Oreochrysum parryi*	B, C	F
Asteraceae	*Senecio serra* Hook.	C	F
Asteraceae	*Solidago multiradiata* Ait.	B	F
Asteraceae	*Taraxacum officinale** Weber ex Wiggers	B, C, L	F
Berberidaceae	*Mahonia repens* (Lindl.) G. Don	C	S
Bryophyta	—	C	F
Campanulaceae	*Campanula parryi* Gray	B	F
Caprifoliaceae	*Distegia involucrata*	B, C	S
Caryophyllaceae	*Spergularia rubra**	L	F
Celastraceae	*Paxistima myrsinites* (Pursh) Raf.	B, C, L	S
Convallariaceae	*Maianthemum stellatum* (L.) Link	C	F
Cyperaceae	*Carex geyeri*	B, C, L	G
Cyperaceae	*Carex rossi*	B, C, L	G
Cyperaceae	*Carex* sp.	B	G
Ericaceae	*Vaccinium myrtillus* L.	B, C, L	S
Ericaceae	*Vaccinium scoparium* Leib. ex Covill	B, C, L	S
Fabaceae	*Lathyrus leucanthus*	B, C	F
Fabaceae	*Lupinus argenteus*	B, C, L	F
Fabaceae	*Vicia americana* Muhl. Ex Willd.	B, C	F
Fabaceae	*Vicia villosa**	B, C	F
Geraniaceae	*Geranium richardsonii*	B, C	F
Grossulariaceae	*Ribes lacustre* (Pers.) Poir	B	S
Hellboraceae	*Aconitum columbianum* Nutt. Ex Torr. & Gray	B	F
Hellboraceae	*Aquilegia coerulea* James	C	F
Liliaceae	Unknown	B	F
Melanthiaceae	*Toxicoscordion venenosum* (Watson) Rydb.	B	F
Onagraceae	*Chamerion danielsii*	B, C, L	F
Poaceae	*Bromus japonicus**	B	G
Poaceae	*Calamagrostis canadensis*	B, C	G
Poaceae	*Elymus glaucus*	B, C, L	G
Poaceae	*Trisetum spicatum* (L.) Richter	B, L	G
Polemoniaceae	*Collomia linearis*	C	F
Pyrolaceae	*Pyrola minor* L.	C	F
Ranunculaceae	*Ranunculus* sp.	B	F
Rosaceae	*Fragaria virginiana* Miller	B, C	F
Rosaceae	*Potentilla diversifolia* Lehm.	B	F
Rosaceae	*Rosa woodsii*	B, C	S
Rosaceae	*Rubus idaeus*	B, C	S

Table 3 (*concluded*).

Family	Species	Treatment	Growth form
Rosaceae	*Rubacer parviflorum* (Nutt.) Rydb.	B	S
Rubiaceae	*Galium septentrionale* and *Galium trifidum*	B, C	F
Scrophulariaceae	*Castilleja rhexiifolia* Rydb.	B	F
Thalictraceae	*Thalictrum fendleri*	B, C	F
Trilliaceae	*Trillium ovatum* Pursh	C	F

Note: Thirty-eight forbs, nine shrubs, and seven graminoid species were encountered in this study. *Galium septentrionale* and *Galium trifidum* were difficult to differentiate and, thus, were grouped together, as were *Osmorhiza depauperata* and *Osmorhiza chilensis*. A few Asteraceae, Liliaceae, Ranunculaceae, and Cyperaceae were not identified to species because of missing flowering parts. All mosses were grouped into a single Bryophyta category. Nomenclature follows Weber and Wittmann (1996). Treatments are B, blowdown; C, control; and L, salvage logged. Growth forms are F, forb; G, graminoid; and S, shrub.
*Nonnative species.

tend to persist until canopy closure is reestablished (Dion 1998; Halpern and Spies 1995; Noble and Alexander 1977; Zamora 1982). Understory composition of areas salvage logged following the eruption of Mount St. Helens, Washington, remained markedly different from unlogged areas more than 20 years after the logging occurred (Titus and Householder 2007). Logged and unlogged subalpine spruce–fir forests in Wyoming also differed in understory species composition 30–50 years after the logging occurred (Selmants and Knight 2003). These studies suggest that, whereas understory composition can change rapidly in the first few years following disturbance, the effects of disturbance on composition are often long-lasting.

Differences in understory disturbance intensity are likely responsible for the observed differences in composition and diversity between blowdown and salvage-logged areas in this study. Roberts (2004) separates disturbance severity into canopy, understory, and soil components and maintains that understory response to disturbance predictably reflects disturbance severity and ensuing regeneration mechanisms, which are modified by life-history traits of the species assemblage and landscape factors. Following this framework, the blowdown disturbance may be viewed as less severe because, although the canopy was removed, understory and soil layers were disturbed only where trees fell or were uprooted. Consequently, regeneration could proceed through a variety of modes, including extension of existing vegetation, vegetative reproduction, and establishment from seed (Roberts 2004). Mechanized salvage logging removed understory vegetation and part of the organic horizon, as demonstrated by the significantly shallower organic horizon and greater cover of bare soil in salvage-logged areas. Because of this more severe understory disturbance, regeneration in salvage-logged areas may have occurred more from new establishment from seed or seedbank propagules than from vegetative growth of residual understory species, which may have been less abundant than in unlogged blowdown areas. Furthermore, the magnitude of understory disturbance intensity was reflected in the depth of the organic horizon, which was the most strongly correlated variable to the NMS ordination axes. The increase in NMS axis 2 scores and decrease in axis 1 scores of disturbed plots between 2001 and 2002 may reflect the process of rebuilding the organic horizon and the nitrogen stores in this horizon and its effect on floristic composition. Although this study did not empirically test the role of understory and organic horizon disturbance on vegetation dynamics, results were similar to findings from a 7 year study of an experimentally disturbed boreal spruce–fir forest (Rydgren et al. 2004). Rydgren et al. (1998) found that depth of litter and soil disruption were strongly related to floristic composition and rate of understory vegetation succession.

Nonnative species

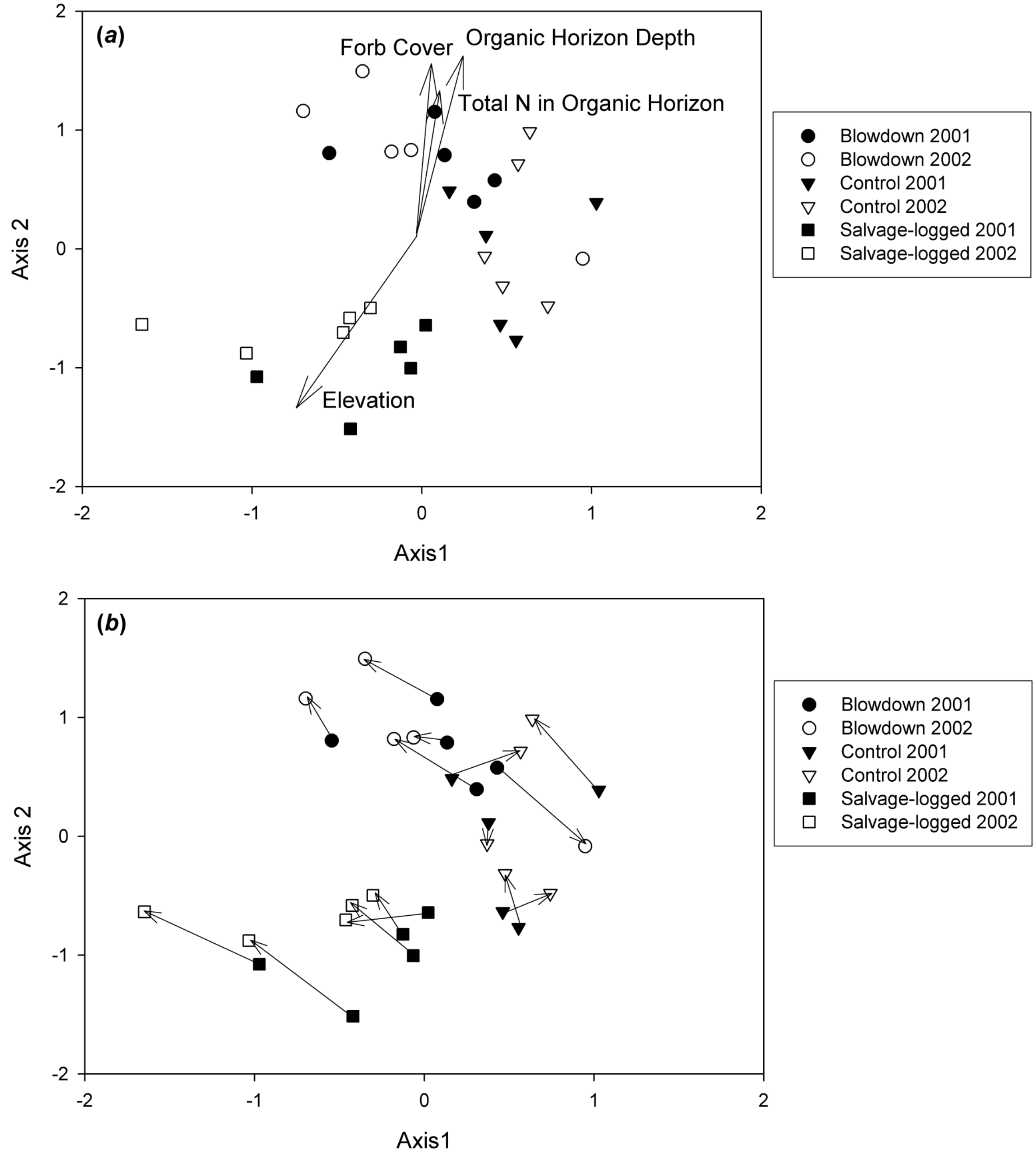
Nonnative species cover was less than 1% in all treatment areas, although 73% of all plots contained at least one nonnative species. Nonnative cover was greater in blowdown areas than in control areas, where total vegetation cover was also greater. Nonnative cover at the 1 m^2 scale is often correlated positively with native cover and species richness in southern Rocky Mountain forests because of greater resource availability in forest areas with greater vegetation cover (Stohlgren et al. 1999). The existence of previously unvegetated microsites, such as root pits, in blowdown areas may also favor the expansion of nonnative species into areas where their predisturbance cover was low. This appears to have been the case with Canada thistle (*Breea arvensis*), which is known to expand its range in response to understory-clearing disturbances (Weaver et al. 2001). Once established, nonnative species can persist in logged spruce–fir forests, albeit in low proportions, for five or more decades (Selmants and Knight 2003).

Potential understory trajectories

Although it is difficult to draw long-term conclusions from the 2 years of data presented here, comparison of diversity and cover values of blowdown areas in this study with results from nearby 15- and 65-year-old blowdowns suggests that diversity will remain enhanced relative to intact forest areas for at least a decade, but understory vegetation cover may decrease during this time (Kulakowski and Veblen 2003; Reid 1989; Savage et al. 1992). In subsequent decades as canopy cover is reestablished, understory vegetation most likely will resemble the understories of mature spruce–fir forests.

More dramatic successional changes are possible in salvage-logged areas. Salvage-logged sites are tending towards graminoid dominance with the twofold increase in proportional graminoid cover between 2001 and 2002, and simultaneous contraction of forb and shrub cover. Death of the understory shrub *Vaccinium* was evident in salvage-

Fig. 2. NMS ordination of plot data by (*a*) treatment category and (*b*) year. In Fig. 2*a*, vectors radiating from the centroid of the ordination reflect the direction and strength of the relationship between environmental variables and ordination scores. The angle of the vector with respect to axis 1 is proportional to the correlation of the listed variable with axis 1. The length of the vector is proportional to the r^2 value of the correlation between the listed variable and both axis 1 and axis 2. Vectors shown here have r^2 values greater than 0.65 with at least one axis. In Fig. 2*b*, arrows connecting points show the shift in community composition of a plot between 2001 and 2002.



logged areas, where *Vaccinium* cover decreased by 35% between 2001 and 2002. *Vaccinium* survived salvage logging only in protected areas around stumps and logs; dead or dying *Vaccinium* was ubiquitous elsewhere. *Vaccinium* cannot survive physical disturbance or soil compaction incurred during logging operations or the harsh environmental conditions of logged areas (Selmants and Knight 2003). The loss of *Vaccinium* from salvage-logged areas may leave areas open for colonization by shade-intolerant, nonforest forbs and graminoids, including nonnative species.

The observed changes in the understory community of salvage-logged areas are of management concern because, in subalpine forests, the understory harbors most of the native plant diversity and understory vegetation can facilitate or constrain spruce seedling establishment (Alexander 1987; Day 1963; Roe et al. 1970). Spruce seedling densities in salvage-logged areas of Routt National Forest were significantly lower than in blowdown areas (Rumbaitis-del Rio 2004). Field observations suggest that establishment of spruce seedlings is favored by *Vaccinium* spp., *Chamerion danielsii*, and *Potentilla* sp., which offer shading and protection without depleting soil moisture (Alexander 1987), whereas sod-forming grasses and *Carex* sp. can preclude spruce establishment through root competition for moisture (Alexander 1984). Proliferation of graminoid species following understory-clearing disturbances such as fire and clearcut logging in subalpine forests can delay conifer seedling establishment and canopy closure for decades to more than a century (Jacobs 2004; Stahelin 1943) in these high-elevation forests, where conifer regeneration is a slow process constrained by seed availability and growth-limiting climate factors (Antos et al. 2000; Eastham and Jull 1999; McCaughey et al. 1991; Noble and Alexander 1977).

Clearly, more research is needed on the long-term dynamics of this system to determine if salvage logging will result in different patterns of succession. Further research should also examine differences in salvage-logging impacts from tractor- versus helicopter-logging systems because these may differ significantly in the depth and extent of understory and soil disturbance. Finally, results presented here must be interpreted with caution because elevation differences between blowdown and salvage-logged treatments may amplify observed treatment differences.

Ultimately, the disturbance caused by salvage logging may alter understory community composition more than the original blowdown. Managers of wind-disturbed forest areas should consider the effects of added understory disturbance on understory vegetation, diversity, and regeneration dynamics before adopting salvage logging as a management tool since the long-term effects are unknown and difficult to predict.

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References

Alexander, R.R. 1984. Natural regeneration of Engelmann spruce after clearcutting in the central Rocky Mountains in relation to environmental factors. USDA For. Serv. Res. Pap. RM-245.

Alexander, R.R. 1987. Ecology, silviculture and management of Engelmann spruce and subalpine fir type in central and southern Rocky Mountains, USA. US Dep. Agric. Agric. Handb. No. 659.

Antos, J.A., Parish, R., and Conley, K. 2000. Age structure and growth of the tree-seedling bank in subalpine spruce–fir forests of south-central British Columbia. Am. Midl. Nat. **143**: 342–354.

Beatty, S.W., and Stone, E.L. 1986. The variety of soil microsites created by tree falls. Can. J. For. Res. **16**: 539–548.

Bellingham, P.J., Tanner, E.V.J., Rich, P.M., and Goodland, T.C.R. 1996. Change in light below the canopy of a Jamaican montane forest after a hurricane. J. Trop. Ecol. **12**: 699–722.

Canham, C.D., and Loucks, O.L. 1984. Catastrophic windthrow in the pre-settlement forests of Wisconsin. Ecology, **65**: 803–809.

Carlton, G.C., and Bazzaz, F.A. 1998. Resource congruence and forest regeneration following an experimental hurricane blowdown. Ecology, **79**: 1305–1319.

Colorado Climate Center. 2003. Climate of Colorado. Atmospheric Sciences Department, Colorado State University, Fort Collins, Colo. Available from http://climate.atmos.colostate.edu/ [accessed 28 October 2003].

Cooper-Ellis, S., Foster, D.R., Carlton, G., and Lezberg, A. 1999. Forest response to catastrophic wind: results from an experimental hurricane. Ecology, **80**: 2683–2696.

Day, R.J. 1963. Spruce seedling mortality caused by adverse summer microclimate in the Rocky Mountains. Can. For. Serv. Res. Branch Publ. No. 1037.

Dion, A.N. 1998. Vegetation response to slash treatment and soil disturbance after clearcutting in a Rocky Mountain conifer forest. MSc. thesis, University of Wyoming, Laramie, Wyo.

Eastham, A.M., and Jull, M.J. 1999. Factors affecting natural regeneration of *Abies lasiocarpa* and *Picea engelmannii* in a subalpine silvicultural systems trial. Can. J. For. Res. **29**: 1847–1855.

Elliott, K.J., Heil, J.W., Kelly, E.F., and Monger, H.C. 1999. Soil structural and other physical properties. *In* Standard soil methods for long-term ecological research. *Edited by* G.P. Robertson, D.C. Coleman, C.S. Bledsoe, and P. Sollins. Oxford University Press, New York. pp. 74–85.

Elliott, K.J., Hitchcock, S.L., and Krueger, L. 2002. Vegetation response to large scale disturbance in a southern Appalachian forest: Hurricane Opal and salvage logging. J. Torrey Bot. Soc. **129**: 48–59.

Everham, E.M., and Brokaw, N.V.L. 1996. Forest damage and recovery from catastrophic wind. Bot. Rev. **62**: 113–185.

Fischer, A., Abs, G., and Lenz, F. 1990. Natural development of forest stands following windfall—approaches to primeval forest research in the Federal Republic of Germany. Forstwiss. Centralblatt, **109**: 309–326.

Foster, D.R., and Boose, E.R. 1992. Patterns of forest damage resulting from catastrophic wind in central New England, USA. J. Ecol. **80**: 79–98.

Gorte, R.W. 1996. Salvage timber sales and forest health. US Cong. Res. Serv. Rep. No. 95-364-ENR.

Halpern, C.B., and Spies, T.A. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecol. Appl. **5**: 913–934.

Jacobs, D.F. 2004. Restoration of a Rocky Mountain spruce–fir forest: sixth-year Engelmann spruce seedling response with or without tree shelter removal. *In* National Proceedings: Forest and Conservation Nursery Associations—2003. *Edited by* L.E. Riley, R.K. Durnroese, and T.D. Landis. USDA Forest Service

Rocky Mountain Research Station, Fort Collins, Colo. Publ. No. RMRS-P-33. pp. 57–63.

Kent, M., and Coker, P. 1996. (*Editors*). The description of vegetation in the field. *In* Vegetation description and analysis: a practical approach. John Wiley & Sons, New York. pp. 28–76.

Kulakowski, D., and Veblen, T.T. 2003. Subalpine forest development following a blowdown in the Mount Zirkel Wilderness, Colorado. J. Veg. Sci. **14**: 653–660.

Lindemann, J.D., and Baker, W.L. 2001. Attributes of blowdown patches from a severe wind event in the southern Rocky Mountains, USA. Landsc. Ecol. **16**: 313–325.

Lindenmayer, D.B., Foster, D.R., Franklin, J.F., Hunter, M.L., Noss, R.F., Schmiegelow, F.A., and Perry, D. 2004. Salvage harvesting policies after natural disturbance. Science (Washington, D.C.), **303**: 1303.

McCaughey, W.W., Fieldler, C.E., and Schmidt, W.C. 1991. Twenty-year natural regeneration following five silvicultural prescriptions in spruce–fir forests of the Intermountain West. USDA For. Serv. Intermountain For. Range Exp. Stn. Res. Pap. INT-439.

McCune, B., and Grace, J.B. (*Editors*). 2002*a*. Species diversity. *In* Analysis of ecological communities. MjM Software Design, Gleneden Beach, Ore. pp. 25–34.

McCune, B., and Grace, J.B. (*Editors*). 2002*b*. Indicator species analysis. *In* Analysis of ecological communities. MjM Software Design, Gleneden Beach, Ore. pp. 198–204.

McCune, B., and Grace, J.B. (*Editors*). 2002*c*. Nonmetric multidimensional scaling. *In* Analysis of ecological communities. MjM Software Design, Gleneden Beach, Ore. pp. 125–142.

McCune, B., and Mefford, M.J. 1999. Multivariate analysis of ecological data, PC-ORD. MjM Software, Gleneden Beach, Ore.

McIver, J.D., and Starr, L. 2000. Environmental effects of post-fire logging: literature review and annotated bibliography. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-486.

Noble, D.L., and Alexander, R.R. 1977. Environmental factors affecting natural regeneration of Engelmann spruce in central Rocky Mountains. For. Sci. **23**: 420–429.

Palmer, M.W., McAlister, S.D., Arevalo, J.R., and DeCoster, J.K. 2000. Changes in the understory during 14 years following catastrophic windthrow in two Minnesota forests. J. Veg. Sci. **11**: 841–854.

Peet, R.K. 1981. Forest vegetation of the Colorado Front Range — composition and dynamics. Vegetatio, **45**: 3–75.

Peterson, C.J., and Campbell, J.E. 1993. Microsite differences and temporal change in plant communities of treefall pits and mounds in an old-growth forest. Bull. Torrey Bot. Club, **120**(4): 451–460.

Peterson, C.J., and Pickett, S.T.A. 1990. Microsite and elevational influences on early forest regeneration after catastrophic windthrow. J. Veg. Sci. **1**: 657–662.

Peterson, C.J., and Pickett, S.T.A. 1995. Forest reorganization — a case-study in an old-growth forest catastrophic blowdown. Ecology, **76**: 763–774.

Reid, M. 1989. The response of understory vegetation to major canopy disturbance in the subalpine forests of Colorado. MSc. thesis, University of Colorado, Boulder, Colo.

Roberts, M.R. 2004. Response of the herbaceous layer to natural disturbance in North American forests. Can. J. Bot. **82**(9): 1273–1283.

Robertson, G.P., Sollins, P., Ellis, B.G., and Lajtha, K. 1999. Exchangeable ions, pH, and cation exchange capacity. *In* Standard soil methods for long-term ecological research. *Edited by* G.P. Robertson, D.C. Coleman, C.S. Bledsoe, and P. Sollins. Oxford University Press, New York. pp. 106–114.

Roe, A.L., Alexander, R.R., and Andrews, M.D. 1970. Engelmann spruce regeneration practices in the Rocky Mountains. USDA For. Serv. Prod. Res. Pap. No. 115.

Rumbaitis-del Rio, C.M. 2004. Compound disturbance in a managed landscape: ecological effects of catastrophic blowdown, salvage-logging, and wildfire in a subalpine forest. Ph.D. thesis, University of Colorado, Boulder, Colo.

Rydgren, K., Hestmark, G., and Okland, R.H. 1998. Revegetation following experimental disturbance in a boreal old-growth *Picea abies* forest. J. Veg. Sci. **9**: 763–776.

Rydgren, K., Okland, R.H., and Hestmark, G. 2004. Disturbance severity and community resilience in a boreal forest. Ecology, **85**: 1906–1915.

SAS Institute Inc. 2001. Statistical analysis software. Version 8.02. SAS Institute Inc., Cary, N.C.

Savage, M., Reid, M., and Veblen, T.T. 1992. Diversity and disturbance in a Colorado subalpine forest. Phys. Geogr. **13**: 240–249.

Schmid, J.M., and Frye, R.H. 1974. Spruce beetle in the Rockies. USDA For. Serv. Gen. Tech. Rep. RM-49.

Scott-Denton, L.E., Sparks, K.L., and Monson, R.K. 2003. Spatial and temporal controls of soil respiration rate in a high-elevation, subalpine forest. Soil Biol. Biochem. **35**: 525–534.

Selmants, P.C., and Knight, D.H. 2003. Understory plant species composition 30–50 years after clearcutting in southeastern Wyoming coniferous forests. For. Ecol. Manage. **185**: 275–289.

Sinton, D.S., Jones, J.A., Ohmann, J.L., and Swanson, F.J. 2000. Windthrow disturbance, forest composition, and structure in the Bull Run basin, Oregon. Ecology, **81**: 2539–2556.

Snyder, G.L., Patten, L.L., and Daniels, J.J. 1987. Mineral resources of the Mount Zirkel Wilderness and northern Park Range vicinity, Jackson and Routt counties, Colorado. US Government Printing Office, Washington, D.C.

Sollins, P., Glassman, C., Eldor, P.A., Swanston, C., Lajtha, K., Heil, J.W., and Elliott, E.T. 1999. Soil carbon and nitrogen pools and fractions. *In* Standard soil methods for long-term ecological research. *Edited by* G.P. Robertson, D.C. Coleman, C.S. Bledsoe, and P. Sollins. Oxford University Press, New York. pp. 89–105.

Spurr, S.H. 1956. Natural restocking of forests following the 1938 hurricane in central New England. Ecology, **37**: 443–451.

Stahelin, R. 1943. Factors influencing the natural restocking of high altitude burns by coniferous trees in the central Rocky Mountains. Ecology, **24**: 19–30.

Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M., and Son, Y. 1999. Exotic plant species invade hot spots of native plant diversity. Ecol. Monogr. **69**: 25–46.

Titus, J.H., and Householder, E. 2007. Salvage logging and replanting reduce understory cover and richness compared to unsalvaged unplanted sites at Mount St. Helens, Washington. West. N. Am. Nat. In press.

Turner, M.G., Romme, W.H., Gardner, R.H., and Hargrove, W.W. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecol. Monogr. **67**: 411–433.

US Congress 2003. Healthy Forest Restoration Act. P.L.108-148.

USDA Forest Service 1999. Final environmental impact statement — North Fork salvage analysis. USDA Forest Service, Hahn's Peak/Bears Ears Ranger District, Steamboat Springs, Colo.

USDA Natural Resources Conservation Service. 2004. The PLANTS database. Version 3.5. Available from http://plants.usda.gov [accessed 1 May 2004].

Van Nieuwstadt, M.G.L., Sheil, D., and Kartawinata, K. 2001. The ecological consequences of logging in the burned forests of east Kalimantan, Indonesia. Conserv. Biol. **15**: 1183–1186.

Veblen, T.T., Hadley, K.S., Reid, M.S., and Rebertus, A.J. 1989. Blowdown and stand development in a Colorado subalpine forest. Can. J. For. Res. **19**: 1218–1225.

Veblen, T.T., Hadley, K.S., Reid, M.S., and Rebertus, A.J. 1991. The response of subalpine forests to spruce beetle outbreak in Colorado. Ecology, **72**: 213–231.

Weaver, T., Gustafson, D., and Lichthardt, J. 2001. Exotic plants in early and late seral vegetation of fifteen northern Rocky Mountain environments (HTs). West. N. Am. Nat. **61**: 417–427.

Webb, S.L. 1999. Disturbance by wind in temperate-zone forests. *In* Ecosystems of disturbed ground. *Edited by* L. Walker. Elsevier Science, Amsterdam. pp. 187–222.

Webb, S.L., and Scanga, S.E. 2001. Windstorm disturbance without patch dynamics: twelve years of change in a Minnesota forest. Ecology, **82**: 893–897.

Weber, W., and Wittmann, R.C. 1996. Colorado flora, western slope. University Press of Colorado, Niwot, Colo.

Wesley, D.A., Poulos, G.S., Meyers, M.P., Snook, J.S., and Judson, A. 1998. Observations and forcing mechanisms during the October 1997 Front Range blizzard and forest destruction. *In* Proceedings of the 8th Conference on Mountain Meteorology, 3–7 August 1998, Flagstaff, Ariz. American Meteorological Society. pp. 25–30.

Zamora, B.A. 1982. Understory development in forest succession: an example from the inland northwest. *In* Proceedings of a Symposium, Forest succession and stand development research in the Northwest, 26 March 1981, Corvallis, Ore. *Edited by* J.E. Means. Forest Research Laboratory, Oregon State University, Corvallis, Ore. pp. 63–69.

Appendix A

Fig. A1. Relationship between depth of the organic horizon and elevation in various spruce–fir stands in the Colorado Rockies. Solid line is the linear regression. Broken lines are 95% confidence intervals for the regression. Symbols denote forest location. RT, Routt National Forest; NW, Niwot Ridge Long Term Ecological Research Station; WR, White River National Forest.

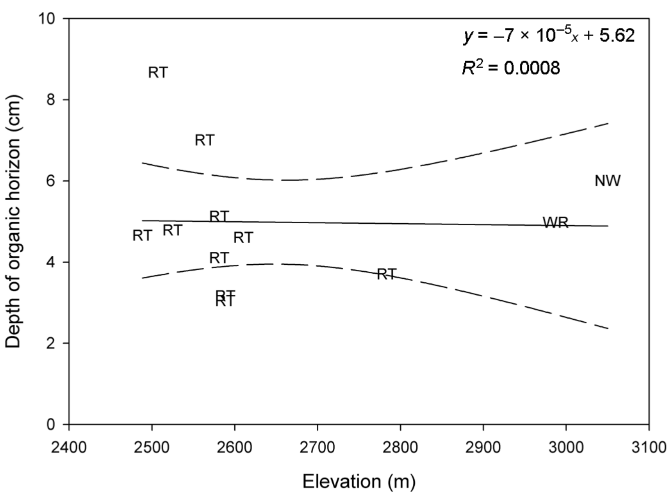

Table A1. Location, mean, and range for each data point.

Location	Elevation (m)	Depth of organic horizon (cm) Mean	Range
Routt NF	2564	7.00	6–10
Routt NF	2610	4.60	2–8
Routt NF	2581	4.10	3–6
Routt NF	2783	3.70	1–6
Routt NF	2507	8.67	9–10
Routt NF	2488	4.65	1–10
Routt NF	2525	4.78	0–11
Routt NF	2581	5.12	1–10
Routt NF	2588	3.04	0–10
Routt NF	2588	3.16	0–8
Niwot Ridge LTER*	3050	6.00	na†
White River NF‡	2987	4.97	0–10

*Scott-Denton et al. (2003). LTER, Long-term Ecological Research Station.

†na, not available.

‡Rumbaitis del Rio, C., and Kulakowski, D., unpublished data. NF, National Forest.